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# VESTIGIAL INSTINCTS IN INSECTS AND OTHER ANIMALS[1]

By WILLIAM MORTON WHEELER

The once widely accepted notion of instinct activities as fixed and immutable processes of inscrutable origin has been definitively discarded and replaced by the view that they, like the organism of which they are an expression, are capable of a considerable degree of individual fluctuation or variability. As James[2] says: "In the instincts of mammals, and even of lower creatures, the uniformity and infallibility, which a generation ago were considered as essential characters, do not exist. The minute study of recent years has found continuity, transition, variation and mistake, wherever it has looked for them, and decided that what is called an instinct is usually only a tendency to act in a way of which the *average* is pretty constant, but which need not be mathematically true." Similar statements have been made by other authors imbued with the importance of the genetic study of animal behavior. H. E. Ziegler says:[3] "All the principles that have been established for the morphological consideration of organs hold good also for the instincts; when we refer to them, we also speak of homology, analogy and parallel development, of individual variation, of natural selection and its purposeful result, of artificial selection and hybridization, of becoming vestigial, of re-

[1] Read before the section of Psychology and Anthropology of the New York Academy of Sciences, Nov. 25, 1907.

[2] The Principles of Psychology, II, New York, Henry Holt, 1890, p. 391, *nota*.

[3] Ueber den Begriff des Instincts. Verhandl. deutsch. zool. Gesell. Leipzig, 1891, p. 134 *et seq.*

version (atavism); both here and there we recognize instances of inhibition of development, of natural and artificial abnormalities." As a rule, however, writers have been most concerned with the development or evolution of instinct activities, and have said little or nothing about their involution or disappearance. Permit me for the present to leave the deadlock of opinion on the origin of instincts, as I have no means of deciding whether these are inherited, mechanized, individually acquired activities as claimed by the Neolamarckians, or spontaneous, congenital mutations as claimed by the Neodarwinians, and let us consider some of the cases of their gradual waning and evanescence.

Darwin seems to have been the first clearly to recognize certain animal instincts as purposeless relicts of once highly purposeful adaptations. He dwells on these cases in connection with the expression of the emotions in man and the effects of domestication on animals. G. H. Schneider summarizes Darwin's observations in connection with his own remarks on vanishing instincts, as follows:[1] "Just as the tenacity of heredity accounts for the transmission of organs which have been functionless and vestigial for generations, so it also transmits vestigial impulses (Triebe), or relations between cognitive acts and impulses, which are now purposeless. I allude especially to the oft-cited case of the dog, which, just before lying down, often turns for some time in a circle, even when it is in a room, and not, like its feral ancestors, in the wilds where this gyration is executed for the purpose of treading down the grass. I would further call to mind certain well-known motions of house-dogs and house-cats, which like their feral allies, try to cover their excrement, even in places where there is no sand. These particulars have been far too little observed in animals, or we should undoubtedly be able to cite many other similar examples. Man, too, is known to have such vestigial impulses. The most familiar of them are what I have called the movements of intimidation. Although in civilized man the instinctive uncovering of the canine tooth in the expresssion of contempt, or of all the teeth in rage, has no longer the purpose of intimidating the enemy by a display of weapons, this habit has nevertheless been retained down to the present time. Similarly the aspirated interjection often uttered in a fit of rage, and so like the 'spitting' of the carnivores, is now purposeless, though the impulse to this form of expression is still generally inherited."

The examples of vestigial instincts cited by Darwin and Schneider all agree in conforming to the definition of instinct

[1] Der Thierische Wille: Leipzig, Ambr. Abel, 1880, p. 418, 419.

as an action performed by all the individuals of a species in a similar manner under like conditions. There is, however, another category of these vestiges which seems to represent a more advanced stage of decay or evanescence, in that they seem to be performed only by certain individuals of the species, in circumscribed portions of its geographical range, and only under very unusual stimuli. In my study of the ants, I have repeatedly come upon instinct vestiges of this character, remains of activities that must once have been of the greatest importance to the species, but have since fallen into desuetude and been overlaid or all but completely replaced by more recently acquired instincts. Cases of this description are most obvious in the parasitic species or in those that have changed their nesting habits within comparatively recent times. Forel has called attention to vestigial slave-making instincts in *Strongylognathus huberi* and *rehbinderi*,[1] ants now living as abject parasites in the nests of *Tetramorium cæspitum*, but in all probability descended from slave-makers like *Polyergus rufescens*, which they still resemble in the peculiar falcate structure of their jaws. *P. rufescens*, too, has its vestigial instincts. The workers of this species are no longer able to take food except from the tongues of their slaves, and perish when these attendants are removed, but the queens have retained to a very slight degree the ability to feed independently. This case, and many others that might be cited, are interesting as proving that the castes in polymorphic insects may show different stages in the decay of the same instinct, a condition obviously correlated with visible differences in physical organization and dependent in ultimate analysis on the physiological division of labor so beautifully developed in these and all other social insects. In other words, we not only find the ants exhibiting vestigial instincts as species, but a certain caste within the species may show vestiges of instincts whose full exercise is the normal prerogative of a different caste. Thus under extraordinary circumstances, the usually sterile worker may lay eggs, like the female, or the female may occasionally forage like the workers or accompany them on their slave-making expeditions. In *Leptothorax emersoni*, an ant that lives with *Myrmica canadensis*, I have observed an even more striking example of an obsolescent feeding instinct. The *Leptothorax* when living with the *Myrmica*—and in a state of nature it is never found except in this association—always obtains its food either from the tongues of its hosts (*i. e.*, by regurgitation), or by licking their oily bodies, but when it is

[1] Strongylognathus Huberi et voisins. Bull. Soc. Ent. Suisse X, 7, 1900, pp. 273-280; Miscellanea Myrmécologiques, Rev. Suisse Zool. XII, 1904, p. 2.

separated from the *Myrmica* in an artificial nest it begins to visit the food dish and feeds, rather awkwardly at first, but eventually quite like the non-parasitic species. In this case an instinct, which would certainly be put down by the casual observer as completely absent, can be resuscitated under the conditions of an artificial experiment.[1]

The nidification of ants and other social insects furnishes several examples of vestigial activities, one of which I have described in detail in a former article.[2] *Cremastogaster lineolata*, a common North American ant, which nests in the ground or in rotting wood, belongs to a largely tropical, arboreal genus, many species of which construct great paper or carton nests, roughly resembling the nests of certain social wasps. On very rare occasions, and in a few localities, however, *C. lineolata*, constructs small carton nests or diminutive "sheds" of the same material over the plant-lice and mealy-bugs on whose saccharine excrement it feeds. This is obviously a feeble reminiscence of formerly well-developed carton-building instincts.

I will cite three other cases of vestigial instincts of nidification. The common honey bee (*Apis mellifera*), which in a state of domestication prefers to suspend its waxen combs in closed hives, readily becomes feral and then nearly always takes up its abode in hollow tree trunks. On very rare occasions, however, it suspends its combs in exposed situations from the branches of trees. The form and position of these combs are so much like those of certain species of *Apis* (*A. dorsata* and *florea*) in southern Asia, where the honey bee lived before it was domesticated and exported to temperate regions, that we are justified in interpreting this very unusual method of nidification as a return to ancestral conditions; in other words, as a revival of a lingering or vestigial instinct, called forth by some unusual stimulus, such as the inability to find a suitable nesting cavity at the proper time and in the proper place. The manifestation of this instinct in temperate regions is worse than purposeless, for it leads to the extinction of the colony on the approach of winter.

This case of the honey bee leads me to the consideration of another comb-building insect, one of our common wasps (*Polistes metrica*), which is also of tropical origin. It has, how-

[1] For an account of the symbiosis of these ants see my papers: The Compound and Mixed Nests of American Ants. Amer. Natur. XXXV, 1901, pp. 431-448; Ethological Observations on an American Ant (Leptothorax Emersoni Wheeler), Arch. f. Psychol. u. Neurol. II, 1903, pp. 1-31, 1 Fig: and Notes on a New Guest-Ant, Leptothorax glacialis, and the Varieties of Myrmica brevinodis Emery. Bull. Wis. Nat. Hist. Soc. V, 1907. pp. 70-83.

[2] The Habits of the Tent-building Ant (Cremastogaster lineolata Say). Bull. Am. Mus. Nat. Hist. XXII, 1906, pp. 1-18. pll. I-VI.

ever, migrated of its own accord into northern regions and has acquired a new series of instincts in adaptation to the great changes of the seasons and the food supply. This insect builds small paper combs and feeds its larvæ on the nectar of flowers and fragments of insects. It does not, as a rule, store up these substances, but uses all the cells of its comb for breeding purposes. In the autumn the colony perishes, with the exception of one or a few fertilized females, which hibernate under the bark of trees, in barns or in the attics of houses and start fresh nests and broods during the ensuing spring. The following observations show that *P. metrica* and some other species of the same genus may exhibit vestiges of instincts once highly developed in their ancestral tropical environment.

November 3, while walking with Professor J. M. Cattell over his estate at Garrison-on-Hudson, I found a number of small nests of *Polistes metrica* hanging from the eaves of a boat-house. These nests were empty and abandoned by the insects, with the exception of one, about 5 cm. in diameter and consisting of a few dozen cells. Four female *Polistes*, inactive with the cold, were clinging to the comb, six of the cells of which contained half grown, much contracted, but still living larvæ. There were small drops of a colorless liquid in many of the other cells and one of them was half full of this substance, which was tasted and proved to be honey of an agreeable flavor. The drops hung suspended in the angles of the cells, but were without any definite arrangement and varied much in size. This honey must have been collected some weeks previously from the autumn flowers and stored, now that nectar and insect food were no longer to be had, for the purpose of bringing the few remaining larvæ to maturity. This belated brood undoubtedly accounted for the presence of the female insects at so advanced a date.

I doubt not that other entomologists have noticed this tendency of our species of *Polistes* to store honey, but the habit is certainly very infrequent. Among the observers who have studied European species of *Polistes* most closely, von Siebold and Ed. André have made no mention of this peculiar instinct. It has, however, been noticed by Lepeletier,[1] Rouget[2] and Marchal.[3] Lepeletier says concerning *Polistes gallica* that "at the time when the comb, in process of construction, contains cells suitable for the education of the males and fertile females, the worker *Polistes* begin to collect the provisions of honey that seem to be necessary for the preparation of the food which is to

[1] Histoire Naturelle des Insects Hyménoptères, I, 1836, p. 496.
[2] Sur les Coleoptères Parasites des Vespides, Dijon, 1837, p. 37.
[3] Observations sur les Polistes. Bull. Soc. Zool. France, XXI, 1896, pp. 15-21, 2 figg.

develop the reproductive powers of these individuals." Rouget, who kept *Polistes* colonies in captivity, found that in the beginning of October, when most of the cells were empty, the insects filled them with a kind of honey, which resembled in color the unrefined sugar with which they had been fed. More explicit observations have been published by Marchal from whose paper the above references are taken. He describes as follows several nests of *P. gallica* var. *diadema* sent him from Lot-et-Garonne, France: "Fifteen nests were sent by my correspondent, the smallest exhibiting 6, the largest 59 cells; all containing as yet only eggs or very young larvæ. Six of them had 5 to 8 cells containing honey. These were situated in the portion of the comb furthest from the pedicel, and the honey was placed on the wall nearest the periphery, about half way between the bottom and the free border of the cell, in the form of a large, colorless drop, adhering to the alveolar wall, and of syrupy consistency and beautiful transparency.

"Microscopic examination revealed in it the existence of a few pollen grains, various foreign bodies, such as certain curved, refractive filaments whose nature could not be determined, spores of rust, the scales of a Lepidopteron, etc., but these bodies were present in small quantity and did not interfere with the transparency of the honey. Its flavor was saccharine and very agreeable. For the most part, the nests containing the honey had reached a stage with more than 30 cells (the smallest had 25, the largest 59); all the nests without honey had 30 cells or less.

"The honey, although generally occurring in cells already furnished with an egg, must evidently represent a provision; for it was precisely the oldest cells, and those nearest the pedicel, containing recently hatched larvæ or eggs ready to hatch, that were destitute of honey. This honey is not, therefore, for the nourishment of the larvæ in the cells in which it is placed, but is simply stored up to be again removed and distributed among the larval colony. I found honey in some cells that contained no eggs or in which the egg had been destroyed or had shriveled to a mere pellicle. This fact seems to point to a beginning specialization on the part of the queen *Polistes* in establishing cells for provisions, but most often, as has been stated, the egg remained intact above the provisions.

"It follows from the preceding observations that *Polistes* is able to collect honey *from the very beginning of founding its nest*, when the queen alone exists. This fact therefore completely precludes the supposition [of Lepeletier] according to which honey is collected by the wasps for the production of the fertile females. All the larvæ of the nest receive nourish-

ment made of the same elements and of a mixed character, that is, both animal and vegetable."

The storing of honey by *P. americanus* in Lower California was recorded several years ago by Brongniart.[1] He says that the nest of this species "always contains larvæ and nymphs, but only during the winter are the cells of the median portion of the comb filled with pale yellow, transparent honey." Some of this honey was sent to the chemist Bertrand, who analyzed it with interesting results.[2] It is known that in general the sweet substance collected by honey bees is composed of almost pure saccharose. This sugar is split up in the proventriculus of the insect into a mixture of dextrose and levulose. It is this mixture, sometimes called invert sugar, accompanied by a small residue of unaltered saccharose, that constitutes ordinary honey. It turns the plane of polarized light to the left. The honey of *Polistes*, on the contrary, turns it to the right, and seems to consist exclusively of dextrose and saccharose without levulose." Bertrand infers from this fact that *Polistes* either does not, like the bees, alter the constitution of the nectar which it collects, or obtains its honey from sources not exploited by the bee. He is inclined to accept the latter alternative, because the honey he analyzed had been stored during the winter. He loses sight of the fact that in Lower California there are always some flowers in bloom during the winter. It seems more probable, therefore, that *Polistes* merely regurgitates the collected nectar into its cells without being able to alter its chemical constitution.

For further light on the instincts of *Polistes* we have to turn to the tropics, especially to America, where we find the metropolis of this and the allied genera of social wasps. Here, in contrast with the single genus *Polistes* represented by a very small number of species in Europe and the United States, we find according to the recent studies of R. von Ihering [3] and Ducke,[4] no less than eighteen genera (*Melissaia* [=*Nectarina*, *Caba*], *Pseudochartergus*, *Chartergus*, *Clypearia*, *Charterginus*, *Parachartergus*, *Polistes*, *Monocanthocnemis*, *Mischocyttaris*, *Synœca*, *Synœcoides*, *Tatua*, *Apoica*, *Leipomeles*, *Polybia*, *Metapolybia*, *Protopolybia*, and *Megacanthopus*), with more than a hundred described species from Brazil alone. This series of

[1] Note sur les Hyménoptères du Genre Polistes recueillis par M. Diguet en Basse-Californie. Bull. Mus. d'Hist. Nat., 1895, p. 37, 38.

[2] Examen du Miel Produit par une Poliste de Basse-Californie. Bull. Mus. d'Hist. Nat., 1895, pp. 38, 39.

[3] As Vespas Sociaes do Brazil: Revista do Museu Paulista, VI, 1904, pp. 97-309, pll. III-VII.

[4] Sobre as Vespidas Sociaes do Pará. Bol. Museu Goeldi., III, 1905, pp. 317-374, pll. I, II.; Prim. Supplemento *ibid.*, IV, 1906, pp. 652-698, pll. I-IV.

forms embraces 17 species of *Polistes* and 36 species of the closely allied genus *Polybia*. All of these insects construct nests with paper combs, and species of several of the genera have long been known to provision these with considerable quantities of honey. Both H.[1] and R. von Ihering[2] have contributed some valuable observations on this and other habits in these insects. Very little honey and that only in drops is stored up by the Brazilian species of *Mischocyttaris* and *Polistes*, but *Melissaia mellifica* provisions its combs with large quantities of this substance. This is true also of *Polybia sericea*, *sylveirae*, *edula*, *occidentalis* and *lechuguana*.

I find in the American Museum of Natural History a large nest of the Mexican *P. occidentalis pygmæa*, donated to the institution by Mr. William Schauss. It is subglobular, about 20 cm. in diameter, of a light ochre brown color and attached to the small branches of a tree. It contains several combs placed one above the other, each comprising hundreds of cells 2.5 mm. in diameter and about 5 mm. deep. The lowermost combs have been removed and many of the upper combs cannot be seen without destroying the outer paper envelope, but each of the visible combs has the cells over a large central area filled with nearly mature larvæ and pupæ. Around these there is a zone of empty cells and then follows, next to the wall of the nest, a zone 2-3 cm. broad of cells filled with a dark brown, inspissated honey of agreeable flavor. According to Mr. Wm. Beutenmüller, the lowermost comb, when removed some time ago, contained no brood but was filled with honey even in the centre. This nest therefore resembles a beehive in having the brood cells in the centre both of the individual combs and of the series of combs, and the honey cells on the periphery.

The honey of the South American wasps seems to be highly toxic, at least in certain localities or in certain seasons. Azara[3] describes cases of poisoning from the honey of the tatú wasp (*Tatua morio*, according to H.. von Ihering) and Auguste de St. Hilaire[4] gives a vivid account of the effect on himself and two companions of eating the honey of the lechuguana wasp (*Polybia lechuguana*) in Uruguay. On this occasion the honey produced pain in the stomach and intense cerebral excitement followed by drowsiness and excessive debility.

The great quantities of honey collected by the tropical wasps are, of course, stores of provisions for the winter, for, as the von

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[1] Biologie der stachellosen Honigbienen Brasiliens. Zool. Jahrb. Abth. f. System. XIX, 1903, pp. 179-287, pll. X-XXII, 8 textfigg.

[2] *Loco citato*.

[3] Voyages dans l'Amérique Méridionale, V, 1, 1809, p. 160.

[4] Relation d'un Empoisonnement causé par le miel de la Guèpe Lecheguana. Ann. Sci. Nat., IV, 1825, pp. 340-344.

Iherings have shown, many of the species, unlike the northern *Polistes*, do not abandon their nests on the approach of the unfavorable season and start new ones in the spring, but continue to add to their combs and keep on raising their brood throughout the year. These naturalists are unquestionably right in deriving the conditions seen in our northern *Polistes* from those of the tropical species. There can be little doubt that *Polistes* has extended its range into North America and Europe since the close of the glacial epoch. The storing of honey for the winter has been discontinued and the life of the species has been saved by a new set of adaptions involving the abandonment of the nest, the temporary suspension of the breeding instincts and the hibernation of a small number of fertilized females. The drops of honey occasionally stored in the nests are all that remains to point to a once very important means of tiding over the flowerless season and preserving the life of the individual colony. Rouget, Brongniart and myself have observed this vestigial instinct only in the autumn, and this would seem to be the most likely time for a feeble display of the old habit. Marchal observed it in the spring. In this case the instinct may have been resuscitated by a protracted spell of cold weather, scarcity of flowers or other conditions simulating the oncoming of winter.

Not only has the honey-storing instinct of our northern *Polistes* been reduced to a feeble and useless vestige by the adaptation of this insect to life in a temperate zone, but the nest-building instincts, when compared with those of the allied tropical wasps, show unmistakable signs of a similar degeneration. In *Polybia* and several other genera the nest consists of a number of combs, each comprising hundreds of cells and the whole is enveloped in a paper involucre as in the circumboreal genus *Vespa*, but in *Polistes* the involucre is no longer constructed and the nest has dwindled to a single comb with comparatively few cells. And this reduction in the size of the nest has led to, or is the result of, a reduction in the size of the colony.

Non-social insects also occasionally exhibit vestigial instincts of nidification. Schröder[1] has recently obtained experimental proof of the existence of these in the caterpillars of a Tineid moth (*Gracilaria stigmatella*), an insect which feeds on the willow and for this purpose conceals itself in a little case made by folding the point of the willow leaf over onto the under side, curling it up and closing any openings with silk. Schröder reared a brood of caterpillars and placed them on willows with

[1] Ueber experimentell erzielte Instinkt-variationen. Verhand. deutsch. Zool. Gesell. 1903. pp. 158-166.

the tips of the leaves cut off or on trees with leaves of a different shape. He found that 84 out of 91 individuals thus deprived of the opportunity of constructing their cases in the normal manner, built cases by rolling up the edges of the leaves. A second generation bred from these insects on leaves with their tips cut off, behaved in the same manner. A third generation was then bred on uncut leaves and of the 19 cases constructed 15 were of the typical or normal form (*i. e.*, with the tip of the leaf folded over), but four were made by rolling up one or both edges of the leaf. From these experiments Schröder concludes that "when the spinning glands are exhausted or when there is no opportunity to construct the case in the typical manner, phylogenetically older instincts, which are still manifested by other species of the genus, are released. Even still older instincts, in fact, the most primitive instincts of the microlepidopterous larvæ, may manifest themselves, as when the larvæ merely conceal themselves between leaves loosely drawn together. Such modified instincts may be repeated by the offspring without a repetition of the stimulus which first caused their appearance."

In the following example we see another simple instinct emerging under very definite conditions that closely simulate the conditions under which the creature's ancestors once lived. The common pond-snails of the genus *Lymnæus* live in shallow water and breathe atmospheric air by means of a lung, *i. e.*, a sac whose walls are lined with blood-vessels. And although these snails are able to take up directly through their integument the oxygen dissolved in the water, they are nevertheless compelled to rise to the surface and renew the air in their lungs at intervals varying from fifteen seconds to several hours, except during the first days of their lives, when they obtain all their oxygen directly from the water.[1] Many years ago F. A. Forel,[2] von Siebold[3] and Pauly[4] found living at the bottom of lakes in Bavaria and Switzerland certain *Lymnæi* that could not, for very obvious reasons, come to the surface to breathe. Forel noticed that snails brought up from a depth of 250 m. in Lakes Leman and Constance had their lungs filled with water, showing that these animals had long since aban-

[1] Walter, The Behavior of the Pond Snail Lymnæus elodes Say. Cold Spring Harbor Monographs VI, March, 1906. pp. 35.

[2] Introduction à l'étude de la faune profonde du lac Léman. Bull. Soc. Vaud. Sci. Nat. X, No. 62, 1869, and Materiaux pour servir à l'étude de la faune profonde du lac Léman. *Ibid.* XIII, No. 72, 1874.

[3] Ueber das Anpassungsvermögen der mit Lungen athmenden Süsswasser-mollusken. Sitzb. math. phys. Cl. K. Akad. Wiss. München 1875, Heft I.

[4] Ueber die Wasserathmung der Limnæiden. Gekrönte Preisschrift. München 1877, pp. 47.

doned the typical pulmonate method of respiration. But when these same snails were placed in shallow water they repeatedly rose to the surface and filled their lungs with air, like the common pond snails. Similar observations were made by Pauly on the snails of Lake Ferchen. These, in fact, definitively abandoned the habit of breathing water with their lungs after they had once had an opportunity to reach the surface. Here we have a sudden adaptation to new conditions in the life of the animal through the artificial resuscitation of an instinct that for generations has been kept in abeyance, an instinct which might properly be designated as vestigial if it were not so perfectly manifested.

A search through the extensive literature of animal behavior would probably yield many additional examples of obsolescent instincts, but the foregoing will suffice for present purposes. They point to the following conclusions, which, I believe, should not be overlooked in the study of comparative psychology.

1. The vestigial instinct action presents itself as an act of racial or phyletic recollection (Mneme, in the sense of Semon[1]) and must, like the representations of individual memory, depend on psychophysical dispositions abiding in latency, just as the visible morphological characters of the adult organism arise from invisible physiological dispositions in the germ-plasm. These dispositions must be inherited with great tenacity and persistency, since vestiges, both instinctive and structural, often remain latent for generations and then suddenly manifest themselves under the stress of extraordinary stimuli.[2] I am not here concerned with the nature of these dispositions in themselves, for they belong to the category of hypothetical postulates or constructions and at present answer their purpose if they enable us to subsume such apparently disparate phenomena as heredity, racial and individual memory under a common point of view.

2. The vestigial instincts obviously represent a part of the

[1] Die Mneme als erhaltendes Princip in Wechsel des organischen Geschehens. Leipzig, Wilh. Engelmann, 1894.

[2] Many of these vestigial manifestations may therefore be regarded as cases of atavism, when they fail to reappear in all generations, but I have avoided the use of this term, because, as Emery has shown (Was ist Atavismus? Verhandl. V. Internat. Zool. Congress. Berlin, 1901 [1902]) it may be understood in two different senses, either as the reappearance by discontinuous heredity of peculiarities belonging to remote ancestors, or as a special potency or faculty which brings about such reappearance. There can, of course, be no objection to the use of the term in the former sense, but its employment in the latter has had a tendency to discredit the whole subject of discontinuous or latent heredity.

animals' endowment, and their manifestation shows that the capacities of even the lower organisms are greater than their ordinary routine behavior might lead us to suppose. I am not aware that any teleological interpretation has been offered for the marvellous persistency of vestigial instincts and structures. At first sight such a conception would seem to involve a contradiction, since it is usually supposed that these vestiges are functionless and purposeless. If all we mean by these words is being no longer able to respond adaptively to a particular set of conditions, the vestigial organ or instinct may indeed be said to conform to this definition. In this sense the honey storing of *Polistes metrica* as an instinctive response to the cold of autumn, is quite purposeless. But there is another and broader sense, in which such vestiges assume a very different dignity. The organism can exist only in a cosmic setting, and this setting is continually and sometimes suddenly changing. Conditions that have once existed may and often do recur after long lapses of time, or what may amount to the same thing, the organism may migrate or extend its range into regions like those inhabited by its remote ancestors. When this occurs a stock of instinct relicts may be of the greatest utility to the organism, for the persistent inheritance of enfeebled tendencies and impulses may then make possible rapid readjustments to the new conditions. For example, if our winters should become milder, or if *Polistes* should extend its range to such subtropical islands as the Bermudas or the Azores, a manifestation of the latent and enfeebled honey-storing instinct might acquire the value of an incipient adaptation and enable the species to survive under conditions unfavorable to hibernation. Similarly, if the Swiss lakes should become shallow through sudden upheaval of their floors, the deep water *Lymnæi* could at once revert to the respiratory habits of their paludicolous ancestors and, should the desiccation continue, they might even become terrestrial like the land Pulmonates. This last possibility suggests that even when conditions merely change without recurring, vestigial organs and instincts may be useful as starting points for entirely new adaptations, for there are not wanting cases of vestiges that have acquired new functions. In our common Dipterous flies, *e. g.*, the halteres, or vestiges of the posterior wings have become sense-organs since they ceased to reinforce the action of the anterior wings in flight; and the vermiform appendix of man is said to have acquired the function of an intestinal tonsil.

3. The foregoing and similar considerations lead me, in conclusion, to a few remarks on the method of studying vestigial instincts and instincts in general. Some Germans and their over-zealous followers in other lands, have come to look

with a certain disdain on all methods of biological research not strictly experimental. I am, of course, willing to concede many of the claims of these authors. It is evident that in all cases like those above cited, vestigial instincts become manifest through the incidence of unusual conditions. When such conditions intervene in the natural environment of an organism, we have one of nature's experiments, when they are devised and applied by the investigator we have the laboratory experiment, but in both cases the emerging instinct can be correctly understood only by an application of the comparative and historical methods. Thus, as we have seen, the honey-storing instinct of our northern *Polistes* cannot be satisfactorily interpreted without recourse to a study of the whole genus or family to which the insect belongs, and a comparison of the instincts displayed by the various species in their normal environment. And the sudden change in the respiratory instincts of the deep water *Lymnæi* is quite incomprehensible without a reference to the habits of the shallow water and terrestrial Pulmonates. The necessity of applying the comparative and historical methods is also shown in many negative cases. When we ask, *e. g.*, why our domestic pigeons no longer alight or nest in trees, or do so only in very rare instances, no amount of experimentation on the nesting habits of these birds can assist us in answering this question. A comparative study, however, shows that the domestic bird is in all probability derived from the rock-pigeon, a form that had developed an instinct to alight and nest only on cliffs or open ground, and this peculiarity, granting the wonderful conservatism and other peculiarities of hereditary transmission, accounts for the negative behavior above mentioned. Similarly, an explanation of the remarkably small size of the colonies of the northern *Polistes*, as contrasted with the populous communities of the tropical *Polybia* and the allied genera, can be obtained only from a comparative phylogenetic study of the various social wasps with reference to their present natural environments. The tendency of some of our workers in animal behavior to pick and choose single, convenient forms for study—a legacy of the morphological regime which has held sway in our biological laboratories—is therefore unfortunate to the extent that it narrows the field of inquiry of the individual investigator. I am convinced that our knowledge of many of the aspects of instinct, like the one I have been considering, would gain immensely by the comparative study of whole genera or families of closely related organisms, for we know of no case in which an instinct is peculiar to a single species (unless it be, perhaps, the human instinct of reason), and of no cases in which two species manifest an instinct in precisely the same manner.